# Variations In Dieot Wood Anatomy: A Global Analysis Based on the Insidewood Database

**Article** *in* IAWA journal / International Association of Wood Anatomists · January 2007

DOI: 10.1163/22941932-90001638



Elisabeth Wheeler
North Carolina State University


Pieter Baas
Naturalis Biodiversity Center

IAWA Journal, Vol. 28 (3), 2007: 229–258

# VARIATIONS IN DICOT WOOD ANATOMY: A GLOBAL ANALYSIS BASED ON THE INSIDEWOOD DATABASE

**E.A. Wheeler**[1], **P. Baas**[2] and **S. Rodgers**[3]

SUMMARY

Information from the InsideWood database (5,663 descriptions) was used to determine the relative abundance of selected IAWA Hardwood List Features, for the whole world and for the broad geographic regions used in the IAWA List. Features that occur in more than 75% of the records are: growth ring boundaries indistinct or absent, diffuse porosity, exclusively simple perforation plates, alternate intervessel pitting, and non-septate fibers. The geographic distribution of vessel element features found in this study is consistent with previous studies: ring porosity is a Northern Hemisphere adaptation; numerous, narrow, short vessel elements are more common in temperate regions than in tropical regions. Element size is related to habit, with few wide vessels being a syndrome that is virtually absent from shrubs and small trees. The co-occurrence of selected features, ones that earlier have been suggested to be correlated, was examined; *e.g.*, tangential vessel arrangement and ring porosity, rare axial parenchyma and septate fibers, tracheids and exclusively solitary vessels that are of medium to wide diameter. Axial parenchyma features show geographic variation, with aliform to confluent parenchyma and bands more than 3 cells wide being primarily tropical in occurrence. Storied rays, crystals, and silica bodies are more common in the tropics than in the temperate Northern Hemisphere. For ray features, geographic patterns are less apparent. In Australia, incidences of some features (vestured pits, solitary vessels, radial/diagonal vessel arrangement) are influenced by the Myrtaceae being a major component of the flora. This paper is but a general overview. Information from the InsideWood database when combined with detailed information on ecological and geographical distributions of species, and subjected to more robust statistical analyses can be used to address a variety of questions on the evolution of wood structure and the ecological and phylogenetic significance of suites of features.

***Key words:*** Ecological wood anatomy, wood variation, xylem anatomy, vessel diameter and density, axial parenchyma, ray parenchyma, fibers.

---

1) Department of Wood and Paper Science, North Carolina State University, Raleigh, NC 27695-8005, USA (E-mail: elisabeth_wheeler@ncsu.edu].

2) National Herbarium of the Netherlands, P.O. Box 9514, 2300 RA, Leiden, The Netherlands.

3) D.H. Hill Library, North Carolina State University, Raleigh, NC 27695-7111, USA.

*Associate Editor: Steven Jansen*

## INTRODUCTION

There is a long tradition of investigating the incidence of different wood anatomical features as well as their correlations with one another (*e.g.*, Frost 1930, 1931; Metcalfe & Chalk 1950), and with different habitats and environmental parameters (*e.g.*, Bissing 1982; Carlquist 1975, 2001; Baas 1986; Baas & Schweingruber 1987). Sorting out the degree to which this variation reflects phylogenetic or ecologic signals has been and continues to be a challenge (*e.g.*, Carlquist 1975; Lens *et al.* 2004; Lens 2005). More recently assumptions about the functional significance of these variations have been tested experimentally, with particular emphasis on the trade-offs between safety and efficiency of water transport, and most recently, the role of pits and pit membrane structure (*e.g.*, Ewers 1985; Tyree *et al.* 1994; Sperry & Hacke 2004; Hacke *et al.* 2006; Sperry *et al.* 2006). In this paper we use the InsideWood database (5,653 records) to look at the incidence of selected features from the "IAWA List of Microscopic Features for Hardwood Identification" for the whole world and within broadly defined geographic regions. We also look at the co-occurrence of selected features.

*The database* — The starting point for the InsideWood database was the information recorded on marginally perforated cards for the "Anatomy of the Dicotyledons" (Metcalfe & Chalk 1950). Those cards used features considered useful for identification and most features were chosen because they were not of common occurrence (Clarke 1936). This dataset used 86 features, and was computerized in 1981 for searching on a mainframe (Pearson & Wheeler 1981). Subsequently, it was formatted so that it and the GUESS program functioned as a multiple entry identification key on PCs (Wheeler *et al.* 1986; LaPasha & Wheeler 1987). The database was referred to as the OPCN database because the major sources of information were the **O**xford cards of Chalk, with edits using the **P**rinces Risborough key (Brazier & Franklin 1961), atlases published by **C**TFT (Normand & Paquis 1976; Détienne & Jacquet 1983), and descriptions prepared at **N**orth Carolina State, based on post 1950 publications, almost all cited in Gregory (1994), and original observations.

In the late 1990's the 86-feature OPCN database was translated into the 203-feature IAWA List of Features for Hardwood Identification (IAWA Committee 1989). Many features had to be recorded as unknown because there was no information on them in the Oxford list. For example, the only Oxford feature for intervessel pit size was "minute pits" (<4 μm across), while the IAWA Hardwood List uses four categories for pit size (minute: <4 μm; small: 4–7 μm; medium: 7–10 μm; large: >10 μm). In the initial translation, if the OPCN record did not have minute pits, then it was not known whether the wood has small, medium, or large intervessel pits, so these features were recorded as unknowns (25? 26? 27?). More details on the translation are available in the "About the Project" section on the InsideWood web site (http://insidewood.lib.ncsu.edu/search).

The InsideWood database has wide geographic and broad taxonomic coverage (258 families, 2,453 genera, as of November 1, 2006) and includes descriptions of trees, shrubs, and vines. We are working to have names that agree with APG II (2003) and as used on the Angiosperm Phylogeny website (Stevens 2001 onwards). This paper's discussion is based on the database as it was on November 1, 2006, at which time there

Table 1. IAWA Hardwood List: Geographical distribution features.

- 164. Europe and Temperate Asia
  - 165. Europe, excluding Mediterranean
  - 166. Mediterranean including Northern Africa and Middle East
  - 167. Temperate Asia (China), Japan, USSR
- 168. Central South Asia
  - 169. India, Pakistan, Sri Lanka
  - 170. Burma
- 171. Southeast Asia and the Pacific
  - 172. Thailand, Laos, Vietnam, Cambodia (Indochina)
  - 173. Indomalesia: Indonesia, Singapore, Papua New Guinea, and Solomon Islands
  - 174. Pacific Islands (including New Caledonia, Samoa, Hawaii, and Fiji)
- 175. Australia and New Zealand
  - 176. Australia
  - 177. New Zealand
- 178. Tropical mainland Africa and adjacent islands
  - 179. Tropical Africa
  - 180. Madagascar & Mauritius, Réunion & Comores
- 181. Southern Africa (south of the Tropic of Capricorn)
- 182. North America, north of Mexico
- 183. Neotropics and Temperate Brazil
  - 184. Mexico and Central America
  - 185. Caribbean
  - 186. Tropical South America
  - 187. Southern Brazil
- 188. Temperate South America including Argentina, Chile, Uruguay, and S. Paraguay

were 5,663 descriptions. We intend to continue editing the database, using descriptions in the literature (pre-1995 publication drawn from Gregory 1994) and additional observations, either of slides or of the images provided to the InsideWood site. Rodgers *et al.* (2005) provide details about the programming and structure for the InsideWood web site, including the search strategy and image presentation.

*Geographic regions* — The IAWA Hardwood Feature List uses broad geographic regions as defined by Brazier and Franklin (1961) with some regions further subdivided (Table 1). Given that the regions are broad and include a variety of environments it is only possible to make very general statements about the ecological associations of the wood anatomical features. North America (feature 182) and Temperate Asia (167) especially include a broad range of environments and climatic regimes. The bulk of the descriptions for Temperate South America (feature 188) are based on Tortorelli's (1956) work on Argentinean woods and at least one-third of the species might be better considered as subtropical to tropical, so that calling the region of IAWA Feature 188 Temperate is somewhat of a misnomer.

*Data coding and percentages* — In the database features are coded as variable (v) if the feature is present in some samples of a species and absent in others (as is often the case for crystal occurrence), if there is tendency for that feature to be present (as a tendency towards a radial to oblique vessel arrangement), or if it is near the borderline for a definition of a feature (*e.g.,* a wood with 85 % solitary vessels is recorded as variable, 9v, for exclusively solitary vessels, which is defined as >90 % vessels solitary). A feature is coded as unknown (?) when it is not known whether it is present or absent in a wood because the publication used to create the entry did not have information on that feature. For example, many wood anatomical atlases do not give information about vessel element or fiber lengths. This means that for many features the percentage occurrences we report are based on different reference numbers. All descriptions have perforation plate type recorded, so percentages for that feature are based on 5,663 records, but incidence of vessel elements longer than 800 µm is a percentage of 3,911 records as 1,752 records do not have information on vessel element length. For woods with exclusively solitary vessels, information on intervessel pitting arrangement and pit size often was not available because common vessel walls are rare and intervessel pits were not observed. Percentages for intervessel pitting arrangement and size are based on only those woods that had information on those features. When a feature is variable, we treated that as contributing 0.5 to the count. For a related group of features (*e.g.*, porosity, vessel diameter and density) and for habit, the percentages total more than 100 % as some samples of a species may have mean tangential diameters of less than 100 µm, while others have mean tangential diameters of 100–200 µm; therefore both features are recorded as present. Similarly, in some localities a species may be a shrub, while in other localities it is a tree. For computing the incidences of vessel diameter classes for trees, small trees, and shrubs, species with 189 (tree) or 190 (shrub) coded as variables were counted as being small trees.

Table 2 presents the percentage occurrences of selected features for the world as a whole, and for IAWA feature list regions 165, 166, 167, 168, 171, 176, 177, 179, 180, 181, 182, 183, and 188. Percentages for the subdivisions of 164 (Europe and Temperate Asia) are given as the Mediterranean and North Africa (166) have a distinctive climate, and we are interested in how Temperate Europe (165) and Asia (167), separately, compare to one another and to North America. Data for Australia and New Zealand, and for Tropical Africa and Madagascar are also presented separately as they are distinctive floristically, and Pierre Detienne's (CIRAD) new information on Madagascar woods provides an opportunity to compare the characteristics of woods from mainland Tropical Africa with those of Madagascar. IAWA features that are not consistently reported in wood anatomical descriptions, as well as many crystal features, are not included in Table 2 (*e.g.*, intervessel pits angular in outline, disjunctive ray parenchyma cell walls, crystal sand) because we do not have confidence that the occurrences of these features in the database are a reasonable representation of these features in woody plants.

*Constraints* — The number of descriptions is not equivalent to the number of species represented. Some descriptions are for multiple species, 675 represent entire genera (*e.g.*, *Astronium* spp., based on information from Terrazas 1994). Some species, usually ones of commercial importance, have 2–3 descriptions that have been kept separate to recognize the different publications used as sources for the descriptions. For example, there are two descriptions for *Morus alba*, one based on a publication by Ter Welle, Koek-Noorman, and Topper (1986), and another based on a publication by Fahn, Werker, and Baas (1986); the descriptions differ slightly because of different provenances of the materials studied. In this paper, we compare the incidence of features within the broad geographic regions used in the Hardwood List. During editing of the database the intent was to record only the geographic region to which a species is native, but not all records may have been corrected to reflect only the native range, rather than regions where a species was introduced and a wood sample collected.

*Statistics* — For investigating the correlations between selected features, we took a simple approach and prepared contingency tables showing observed co-occurrences, expected co-occurrences based on the individual feature's occurrence, and percentage deviations of observed co-occurrences from expected co-occurrences if the characters were assorted randomly. These tables were prepared using the tools on VassarStats: Web Site for Statistical Computation (http://faculty.vassar.edu/lowry/VassarStats.html) authored by Richard Lowry of Vassar College, Poughkeepsie, New York, and are presented as Tables 3–10.

## INCIDENCE OF FEATURES

***Growth rings*** (Table 2)

Woods with distinct growth ring boundaries are most common in Temperate Europe, Temperate Asia, and North America. For the world as a whole, the incidence of distinct growth ring boundaries is low, 34%. Seasonality in cambial activity is not uncommon in the tropics, but the variations in wood anatomy associated with that seasonality are often different from those of temperate Northern Hemisphere woods (Worbes 1989, 1999; Carlquist 2001). The majority of the records in the InsideWood database are based on descriptions by anatomists trained in the Northern Hemisphere. The incidence of growth ring boundaries reported as distinct, indistinct, or absent is likely linked to this bias.

***Porosity, Arrangement, Grouping*** (Fig. 1 & 2, Table 2)

The default pattern for woody dicots is diffuse porosity (92%) with vessels not in any particular pattern (83%), and occurring as a mixture of solitary vessels and vessels in short multiples (66%) (Fig. 1, Table 2). The latter two percentages are derived by subtracting the combined incidences of features 6, 7, and 8 for vessel arrangement (17%) and features 9, 10, and 11 (34%) for vessel grouping from 100%.

Plotting the incidence of porosity types onto the geographic regions used by the IAWA hardwood list shows that ring porosity is relatively common in north temperate zones, and near-absent in the tropics and Southern Hemisphere, even in Temperate South America and New Zealand (Fig. 2). Gilbert (1940) commented on the absence of ring porosity in the Southern Hemisphere. Ring porous wood occurred in the Cretaceous of Antarctica (Poole *et al.* 2000), so the present-day rarity of this strategy in the Southern Hemisphere is somewhat surprising. An obvious question is whether this difference in incidence of ring porosity between temperate regions of Northern and

Table 2. — Incidence (%) of selected IAWA Hardwood List features for the world and selected geographic regions: Mediterranean including Africa and the Middle East (Med) – Temperate Europe, excluding the Mediterranean (TmpEu) – Temperate Asia (TmpAs) – North America, north of Mexico (NAm) – Central South Asia, including Pakistan, India, Sri Lanka, and Burma (India) – Southeast Asia and the Pacific (SEAsia) – Australia (Aus) – New Zealand (NewZ) – Tropical Africa (TrpAfr) – Madagascar (Madg) – Southern Africa, south of the Tropic of Capricorn (SAfr) – Neotropics (NeoTrp) – Temperate South America, including Chile, Argentina, South Paraguay, and Uruguay (TmpSAm).

| **Geographic region:** | World | Med | TmpEu | TmpAs | NAm | India | SEAsia | Aus | NewZ | TrpAfr | Madg | SAfr | NeoTrp | TmpSAm |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of descriptions per region: | 5663 | 216 | 92 | 496 | 330 | 541 | 1273 | 334 | 128 | 708 | 599 | 103 | 1695 | 248 |
| **Growth rings** | | | | | | | | | | | | | | |
| 1. Boundaries distinct | 34 | 72 | 85 | 84 | 81 | 38 | 24 | 34 | 61 | 28 | 26 | 46 | 17 | 35 |
| 2. Boundaries indistinct or absent | 75 | 46 | 25 | 25 | 27 | 75 | 86 | 79 | 71 | 82 | 80 | 68 | 89 | 72 |
| **Porosity** | | | | | | | | | | | | | | |
| 3. Ring porous | 5 | 20 | 23 | 21 | 25 | 5 | 1.2 | 0.8 | 3 | 0.5 | 1.5 | 1.9 | 1.2 | 3 |
| 4. Semi-ring porous | 8 | 33 | 38 | 22 | 24 | 7 | 3.3 | 6 | 19 | 1.9 | 5 | 6 | 2.7 | 13 |
| 5. Diffuse porous | 92 | 70 | 66 | 70 | 63 | 94 | 97 | 96 | 89 | 98 | 96 | 93 | 97 | 89 |
| **Vessel arrangement** | | | | | | | | | | | | | | |
| 6. Tangential bands | 3 | 9 | 13 | 10 | 14 | 3 | 1.2 | 1.2 | 13 | 1.3 | 0.8 | 5 | 1.2 | 8 |
| 7. Diagonal and/or radial pattern | 11 | 20 | 14 | 15 | 19 | 6 | 7 | 26 | 12 | 9 | 7 | 13 | 10 | 14 |
| 8. Dendritic pattern | 3 | 12 | 9 | 5 | 11 | 0.7 | 0.8 | 3 | 5 | 1.1 | 1.8 | 5 | 2.0 | 7 |
| **Vessel groupings** | | | | | | | | | | | | | | |
| 9. Exclusively solitary (90% +) | 16 | 9 | 22 | 21 | 17 | 12 | 16 | 37 | 16 | 13 | 15 | 23 | 12 | 12 |
| 10. Radial multiples of 4 or more common | 10 | 14 | 13 | 10 | 16 | 13 | 10 | 13 | 11 | 10 | 7 | 17 | 9 | 13 |
| 11. Clusters common | 8 | 29 | 20 | 17 | 6 | 8 | 5 | 7 | 29 | 4 | 2 | 7 | 5 | 16 |
| **Perforation plates** | | | | | | | | | | | | | | |
| Simple (13) only | 82 | 89 | 61 | 53 | 70 | 86 | 80 | 81 | 63 | 88 | 91 | 83 | 87 | 85 |
| Scalariform (14) only | 10 | 6 | 21 | 35 | 21 | 9 | 13 | 10 | 18 | 6 | 4 | 12 | 7 | 8 |
| Simple + scalariform (13 + 14) | 7 | 5 | 18 | 12 | 10 | 5 | 8 | 9 | 19 | 6 | 5 | 6 | 6 | 7 |
| **Intervessel pits: arrangement** | | | | | | | | | | | | | | |
| 20. Scalariform | 8 | 3.9 | 14 | 21 | 12 | 7 | 12 | 12 | 27 | 5 | 3.2 | 6 | 5 | 6 |
| 21. Opposite | 11 | 11 | 19 | 29 | 20 | 8 | 12 | 14 | 37 | 6 | 2.6 | 9 | 7 | 12 |
| 22. Alternate | 91 | 95 | 87 | 76 | 86 | 92 | 88 | 87 | 77 | 95 | 96 | 93 | 94 | 90 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Intervessel pit size: alternate and opposite** | | | | | | | | | | | | | | |
| 24. Minute (4 µm or less) | 27 | 30 | 16 | 20 | 25 | 29 | 28 | 29 | 19 | 33 | 27 | 40 | 28 | 28 |
| 25. Small (4–7 µm ) | 46 | 65 | 56 | 56 | 57 | 42 | 45 | 47 | 72 | 43 | 43 | 45 | 44 | 45 |
| 26. Medium (7–10 µm ) | 40 | 34 | 41 | 44 | 50 | 42 | 40 | 31 | 41 | 39 | 38 | 30 | 42 | 31 |
| 27. Large (10 µm or more) | 19 | 10 | 16 | 14 | 16 | 25 | 21 | 15 | 17 | 17 | 15 | 8 | 22 | 17 |
| **Vestured pits** | | | | | | | | | | | | | | |
| 29. Vestured pits present | 28 | 21 | 2,7 | 5 | 12 | 33 | 26 | 37 | 20 | 35 | 31 | 29 | 30 | 29 |
| **Vessel-ray pitting** | | | | | | | | | | | | | | |
| 30. With distinct borders; similar to intervessel pits in size & shape (all) | 68 | 85 | 79 | 69 | 78 | 62 | 58 | 59 | 60 | 74 | 73 | 78 | 68 | 70 |
| 31. With reduced borders to simple; pits round or angular | 31 | 21 | 29 | 26 | 22 | 39 | 41 | 42 | 47 | 28 | 18 | 24 | 30 | 31 |
| 32. With reduced borders to simple; pits horizontal to vertical | 31 | 15 | 24 | 26 | 16 | 34 | 40 | 44 | 44 | 28 | 25 | 24 | 32 | 27 |
| **Helical thickenings** | | | | | | | | | | | | | | |
| 36. Helical thickenings in vessel elements present | 12 | 36 | 57 | 49 | 40 | 8 | 7 | 7 | 32 | 2.3 | 1.6 | 7 | 3.9 | 13 |
| **Mean tangential diameter of vessel lumina** | | | | | | | | | | | | | | |
| ***For diffuse porous*** | | | | | | | | | | | | | | |
| 40. < 50 µm | 20 | 48 | 75 | 64 | 54 | 11 | 11 | 18 | 42 | 13 | 15 | 38 | 15 | 26 |
| 41. 50–100 µm | 49 | 66 | 73 | 59 | 67 | 40 | 46 | 55 | 61 | 42 | 57 | 65 | 46 | 66 |
| 42. 100–200 µm | 46 | 23 | 7 | 11 | 12 | 54 | 55 | 48 | 19 | 53 | 40 | 33 | 51 | 33 |
| 43. > 200 µm | 12 | 1.3 | 0.0 | 0.6 | 5 | 22 | 17 | 10 | 2.6 | 19 | 3 | 6 | 13 | 5 |
| ***For diffuse, semi-ring and ring porous*** | | | | | | | | | | | | | | |
| 40. < 50 µm | 20 | 41 | 63 | 45 | 47 | 11 | 12 | 18 | 42 | 13 | 16 | 38 | 16 | 29 |
| 41. 50–100 µm | 49 | 64 | 59 | 52 | 58 | 39 | 46 | 54 | 64 | 42 | 58 | 65 | 46 | 67 |
| 42. 100–200 µm | 46 | 26 | 14 | 22 | 22 | 55 | 53 | 48 | 17 | 54 | 43 | 33 | 52 | 31 |
| 43. 200 µm or more | 13 | 5 | 9 | 9 | 12 | 23 | 17 | 9 | 2 | 19 | 4 | 7 | 12 | 4 |

*(Table 2 continued)*

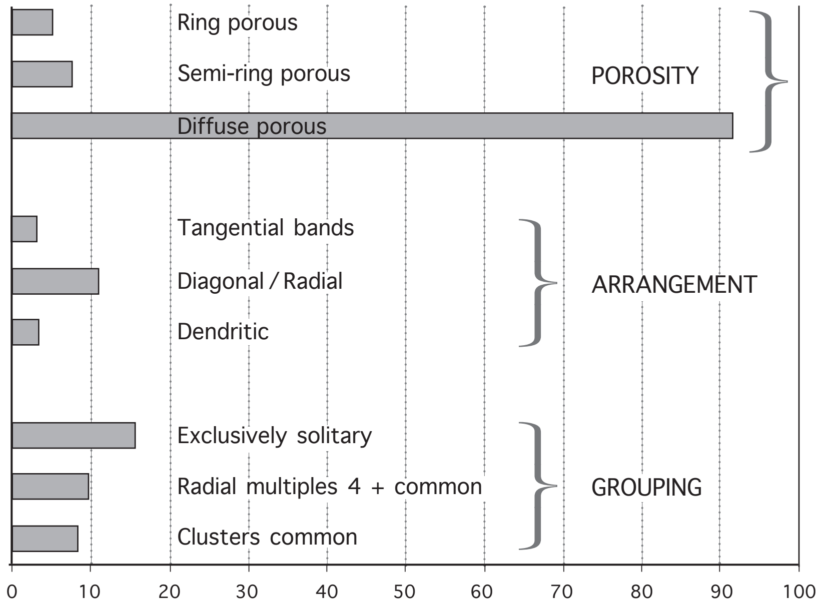
| **Geographic region**<br>Number of descriptions per region | World<br>5663 | Med<br>216 | TmpEu<br>92 | TmpAs<br>496 | NAm<br>330 | India<br>541 | SEAsia<br>1273 | Aus<br>334 | NewZ<br>128 | TrpAfr<br>708 | Madg<br>599 | SAfr<br>103 | NeoTrp<br>1695 | TmpSAm<br>248 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Vessels per square millimeter** | | | | | | | | | | | | | | |
| ***Diffuse porous only*** | | | | | | | | | | | | | | |
| 46. 5 or less | 23 | 5 | 0.0 | 2.6 | 3 | 31 | 11 | 17 | 8 | 34 | 16 | 11 | 27 | 13 |
| 47. 5–20 | 54 | 19 | 6 | 14 | 16 | 67 | 63 | 57 | 36 | 65 | 50 | 35 | 58 | 44 |
| 48. 20–40 | 27 | 28 | 17 | 25 | 31 | 27 | 29 | 30 | 26 | 25 | 30 | 35 | 25 | 33 |
| 49. 40–100 | 18 | 43 | 42 | 45 | 47 | 14 | 13 | 16 | 38 | 13 | 15 | 28 | 15 | 25 |
| 50. 100 or more | 9 | 29 | 63 | 45 | 37 | 6 | 5 | 7 | 31 | 3 | 9 | 14 | 4 | 16 |
| **Mean vessel element length** | | | | | | | | | | | | | | |
| 52. 350 µm or less | 27 | 77 | 39 | 31 | 47 | 38 | 16 | 22 | 22 | 24 | 14 | 22 | 24 | 53 |
| 53. 350–800 µm | 58 | 28 | 68 | 55 | 56 | 66 | 68 | 68 | 67 | 68 | 76 | 74 | 66 | 49 |
| 54. 800 µm or more | 18 | 3 | 6 | 27 | 15 | 14 | 30 | 22 | 18 | 17 | 23 | 17 | 18 | 9 |
| **Tyloses and deposits in vessels** | | | | | | | | | | | | | | |
| 56. Tyloses common | 17 | 8 | 9 | 11 | 12 | 23 | 19 | 30 | 5 | 16 | 15 | 14 | 16 | 15 |
| 57. Tyloses sclerotic | 1.2 | 0.5 | 0.0 | 0.3 | 0.8 | 0.2 | 1.1 | 1.2 | 0.0 | 1 | 0.3 | 1.4 | 2.4 | 1.2 |
| 58. Gums and other deposits in heartwood vessels | 18 | 25 | 20 | 11 | 20 | 29 | 18 | 27 | 18 | 25 | 5 | 17 | 19 | 17 |
| **Imperforate tracheary elements** | | | | | | | | | | | | | | |
| 60. Vascular/vasicentric tracheids present | 12 | 38 | 28 | 38 | 20 | 11 | 8 | 34 | 23 | 7 | 5 | 10 | 9 | 10 |
| **Ground tissue fiber pits** | | | | | | | | | | | | | | |
| 61. Simple to minutely bordered | 73 | 76 | 54 | 55 | 67 | 78 | 71 | 52 | 63 | 79 | 79 | 71 | 79 | 82 |
| 62. Distinctly bordered | 30 | 29 | 54 | 49 | 37 | 24 | 31 | 50 | 44 | 23 | 24 | 35 | 24 | 22 |
| 63. Common in both radial and tangential walls | 23 | 34 | 47 | 41 | 37 | 19 | 26 | 26 | 37 | 19 | 6 | 34 | 20 | 19 |
| **Septate fibers** | | | | | | | | | | | | | | |
| 65. Septate fibers present | 25 | 10 | 9 | 14 | 12 | 26 | 25 | 19 | 43 | 24 | 28 | 30 | 29 | 27 |
| 66. Non-septate fibers present | 85 | 97 | 97 | 93 | 95 | 84 | 84 | 89 | 82 | 85 | 81 | 81 | 80 | 86 |

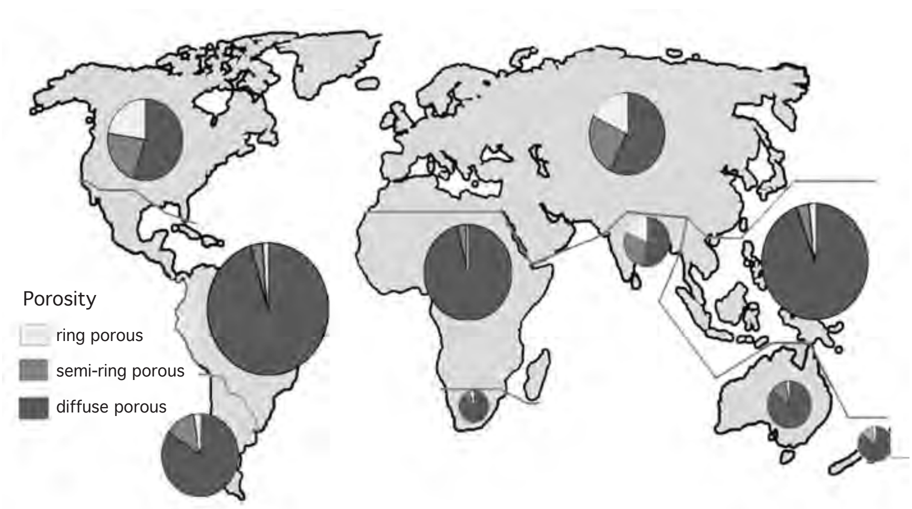
| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Fiber wall thickness** | | | | | | | | | | | | | | |
| 68. Very thin-walled | 11 | 9 | 18 | 16 | 13 | 12 | 18 | 9 | 8 | 8 | 8 | 5 | 9 | 8 |
| 69. Thin to thick-walled | 66 | 84 | 80 | 87 | 76 | 72 | 72 | 64 | 76 | 61 | 80 | 62 | 58 | 60 |
| 70. Very thick-walled | 36 | 36 | 32 | 17 | 31 | 35 | 30 | 41 | 30 | 48 | 36 | 46 | 44 | 40 |
| **Mean fiber lengths** | | | | | | | | | | | | | | |
| 71. 900 µm or less | 27 | 78 | 60 | 34 | 50 | 27 | 17 | 26 | 41 | 19 | 24 | 40 | 26 | 51 |
| 72. 900–1600 µm | 65 | 31 | 60 | 57 | 56 | 79 | 72 | 70 | 64 | 77 | 77 | 72 | 71 | 66 |
| 73. 1600 µm or more | 14 | 3 | 7 | 21 | 6 | 18 | 30 | 11 | 11 | 19 | 12 | 3 | 14 | 4 |
| **Axial parenchyma** | | | | | | | | | | | | | | |
| 75. Absent or extremely rare | 14 | 16 | 28 | 17 | 21 | 9 | 12 | 12 | 20 | 8 | 18 | 25 | 14 | 33 |
| **Apotracheal axial parenchyma** | | | | | | | | | | | | | | |
| 76. Diffuse | 34 | 38 | 57 | 49 | 41 | 38 | 39 | 51 | 56 | 27 | 26 | 33 | 24 | 33 |
| 77. Diffuse-in-aggregates | 19 | 15 | 32 | 30 | 18 | 20 | 24 | 20 | 31 | 15 | 20 | 13 | 14 | 10 |
| **Paratracheal axial parenchyma** | | | | | | | | | | | | | | |
| 78. Scanty paratracheal | 30 | 50 | 25 | 37 | 32 | 32 | 36 | 32 | 61 | 20 | 34 | 32 | 23 | 24 |
| 79. Vasicentric | 32 | 34 | 15 | 25 | 29 | 45 | 38 | 39 | 29 | 35 | 21 | 29 | 31 | 38 |
| 80. Aliform | 19 | 9 | 4 | 7 | 11 | 26 | 20 | 12 | 4 | 28 | 21 | 14 | 21 | 19 |
| 83. Confluent | 19 | 3 | 11 | 13 | 14 | 28 | 18 | 14 | 14 | 26 | 12 | 16 | 21 | 29 |
| **Banded parenchyma** | | | | | | | | | | | | | | |
| 85. Bands >3 cells wide | 9 | 5 | 0.0 | 2.2 | 3 | 10 | 9 | 7 | 7 | 12 | 15 | 8 | 9 | 8 |
| 86. Narrow bands ≤ 3 cells wide | 20 | 5 | 7 | 10 | 12 | 19 | 25 | 20 | 4 | 26 | 13 | 17 | 25 | 15 |
| 89. Marginal or ~marginal bands | 20 | 26 | 24 | 24 | 30 | 24 | 14 | 11 | 21 | 21 | 34 | 14 | 18 | 16 |
| **Axial parenchyma cell type / strand length** | | | | | | | | | | | | | | |
| 90. Fusiform cells | 6 | 34 | 2.2 | 3 | 7 | 3.6 | 2.6 | 2.0 | 8 | 4 | 5 | 1.0 | 6 | 10 |
| 91. Two cells | 31 | 66 | 34 | 26 | 40 | 34 | 23 | 25 | 51 | 34 | 24 | 37 | 32 | 52 |
| 92. Four (3–4) | 67 | 58 | 72 | 65 | 71 | 77 | 70 | 72 | 73 | 68 | 57 | 75 | 70 | 71 |
| 93. Eight (4–8) | 48 | 31 | 55 | 61 | 52 | 53 | 60 | 63 | 54 | 51 | 31 | 46 | 45 | 33 |
| 94. Over 8 | 11 | 3 | 9 | 12 | 11 | 11 | 17 | 7 | 10 | 14 | 6 | 6 | 9 | 5 |

*(Table 2 continued)*

| **Geographic region**<br>Number of descriptions per region | World<br>5663 | Med<br>216 | TmpEu<br>92 | TmpAs<br>496 | NAm<br>330 | India<br>541 | SEAsia<br>1273 | Aus<br>334 | NewZ<br>128 | TrpAfr<br>708 | Madg<br>599 | SAfr<br>103 | NeoTrp<br>1695 | TmpSAm<br>248 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Ray width** (cell number) | | | | | | | | | | | | | | |
| 96. Exclusively uniseriate | 15 | 9 | 13 | 8 | 12 | 15 | 14 | 15 | 4 | 13 | 20 | 13 | 18 | 13 |
| 97. 1 to 3 | 49 | 44 | 45 | 44 | 48 | 40 | 48 | 52 | 31 | 51 | 58 | 44 | 49 | 48 |
| 98. Larger rays commonly 4 to 10 | 36 | 41 | 40 | 45 | 42 | 45 | 40 | 31 | 50 | 35 | 27 | 3 | 32 | 35 |
| 99. Larger rays commonly > 10-seriate | 5 | 14 | 16 | 8 | 7 | 4 | 5 | 4 | 18 | 4 | 4 | 6 | 4 | 5 |
| 100. Rays with multiseriate portion(s) as wide as uniseriate portions | 4 | 1.9 | 3 | 2 | 1.5 | 5 | 6 | 2.1 | 0.8 | 4 | 0.5 | 6 | 5 | 2.4 |
| **Aggregate rays** | | | | | | | | | | | | | | |
| 101. Aggregate rays | 1 | 3 | 5 | 4 | 3 | 0.4 | 0.6 | 3 | 2 | 0 | 2 | 1 | 0.7 | 1.2 |
| **Ray height** | | | | | | | | | | | | | | |
| 102. Ray height > 1 mm | 27 | 29 | 25 | 27 | 21 | 25 | 38 | 23 | 37 | 27 | 11 | 27 | 29 | 17 |
| **Rays of two distinct sizes** | | | | | | | | | | | | | | |
| 103. Rays of two distinct sizes | 11 | 6 | 18 | 17 | 14 | 11 | 14 | 12 | 18 | 7 | 9 | 14 | 10 | 8 |
| **Rays cellular composition** | | | | | | | | | | | | | | |
| 104. All ray cells procumbent | 25 | 22 | 36 | 26 | 34 | 26 | 18 | 26 | 11 | 32 | 27 | 23 | 23 | 34 |
| ***Body ray cells procumbent with marginal rows of upright/square cells*** | | | | | | | | | | | | | | |
| 106. With 1 row | 40 | 44 | 41 | 42 | 46 | 44 | 42 | 43 | 46 | 35 | 31 | 38 | 39 | 47 |
| 107. With 2–4 rows | 39 | 38 | 36 | 44 | 40 | 40 | 44 | 37 | 49 | 34 | 31 | 41 | 38 | 39 |
| 108. With over 4 rows | 30 | 11 | 18 | 29 | 20 | 29 | 37 | 30 | 36 | 28 | 23 | 36 | 32 | 19 |
| **Sheath cells** | | | | | | | | | | | | | | |
| 110. Sheath cells present | 11 | 11 | 13 | 12 | 10 | 12 | 14 | 11 | 20 | 9 | 12 | 13 | 10 | 13 |
| **Rays per mm** | | | | | | | | | | | | | | |
| 114. < 4/mm | 10 | 20 | 15 | 9 | 8 | 10 | 10 | 7 | 14 | 11 | 8 | 12 | 11 | 9 |
| 115. 4–12/mm | 68 | 68 | 52 | 67 | 67 | 71 | 70 | 64 | 76 | 70 | 66 | 59 | 67 | 66 |
| 116. >12/mm | 30 | 24 | 42 | 31 | 33 | 31 | 30 | 35 | 25 | 29 | 34 | 40 | 29 | 30 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Storied structure** | | | | | | | | | | | | | | |
| 118. All rays storied | 4 | 0.5 | 0.5 | 0.7 | 1.8 | 5 | 2.4 | 0.9 | 0.8 | 4 | 11 | 0.5 | 5 | 7 |
| 120. Axial parenchyma and/or vessel elements storied | 10 | 22 | 15 | 6 | 9 | 13 | 7 | 6 | 10 | 9 | 18 | 1.0 | 10 | 15 |
| **Intercellular canals** | | | | | | | | | | | | | | |
| 130. Radial canals | 3.2 | 2.8 | 1.1 | 1.1 | 1.8 | 4.3 | 4.2 | 3.1 | 0.8 | 2.7 | 3.3 | 1.9 | 4.2 | 4.0 |
| 131. Intercellular canals of traumatic origin | 2.2 | 0.7 | 1.6 | 0.7 | 2.0 | 4.1 | 1.3 | 2.3 | 2.3 | 6.2 | 1.2 | 0.0 | 2.5 | 2.2 |
| **Tubes / tubules** | | | | | | | | | | | | | | |
| 132. Laticifers or tanniniferous tubes | 2.6 | 2.1 | 0.0 | 0.5 | 0.6 | 2.2 | 3.3 | 1.5 | 0.8 | 3.1 | 1.2 | 1.9 | 4.5 | 0.8 |
| **Prismatic crystals** | | | | | | | | | | | | | | |
| 136. Prismatic crystals present | 48 | 42 | 20 | 31 | 39 | 52 | 47 | 51 | 24 | 59 | 61 | 58 | 50 | 51 |
| 137. In upright/square ray cells | 18 | 21 | 7 | 16 | 12 | 22 | 20 | 13 | 13 | 18 | 28 | 23 | 19 | 12 |
| 138. In procumbent ray cells | 10 | 16 | 7 | 10 | 11 | 14 | 13 | 9 | 5 | 11 | 7 | 14 | 10 | 9 |
| 140. In chambered upright and/or square cells | 5 | 3.0 | 0.6 | 4.1 | 1.4 | 3.6 | 7 | 5 | 2.7 | 4.5 | 10 | 7 | 5 | 2 |
| 141. In non-chambered axial parenchyma cells | 7 | 7 | 2.8 | 2.9 | 5 | 6 | 8 | 5 | 2.9 | 7 | 12 | 4 | 3 | 6 |
| 142. In chambered axial parenchyma cells | 24 | 17 | 5 | 12 | 19 | 26 | 21 | 26 | 10 | 33 | 33 | 24 | 24 | 28 |
| **Other diagnostic crystal features** | | | | | | | | | | | | | | |
| 156. Crystals in enlarged cells | 3.1 | 6 | 9 | 8 | 5.2 | 3.5 | 3.0 | 3.7 | 2.0 | 2.5 | 3.3 | 3.9 | 2.0 | 4.0 |
| **Silica** | | | | | | | | | | | | | | |
| 159. Silica bodies present | 7 | 1.2 | 0.0 | 0.4 | 0.0 | 5 | 7 | 3.9 | 0.0 | 9 | 9 | 3.9 | 10 | 11.3 |
| **Habit** | | | | | | | | | | | | | | |
| 189. Tree | 84 | 38 | 55 | 69 | 54 | 89 | 87 | 88 | 72 | 89 | 97 | 80 | 87 | 79 |
| 190. Shrub | 20 | 72 | 59 | 37 | 53 | 15 | 18 | 20 | 38 | 15 | 7 | 30 | 16 | 27 |
| 191. Vine/Liana | 3 | 4.2 | 6 | 6 | 3.0 | 3.7 | 3.1 | 2.5 | 0.0 | 2 | 0.0 | 1.4 | 2.8 | – |




Figures 1 & 2. Incidences of qualitative vessel features. – 1: Porosity type, vessel grouping and arrangement as % of the whole database. – 2: Distribution of porosity types by broad geographic region.

Southern Hemispheres is related to differences in leaf longevity, length of growing season, and rainfall patterns. Probably. The native New Zealand "… vegetation, from northern coasts to the alpine limits, is overwhelmingly evergreen" (Wardle 1991: p. 39), and so it is not surprising that ring porous woods are rare in New Zealand. The three New Zealand woods in the database that are ring porous are among the few species that

Wardle (1991) says are deciduous or are almost leafless by the end of the winter. Semi-ring porous woods are more common in Temperate South America, South Africa, and New Zealand than they are in Tropical America, Africa, or Asia where diffuse porous woods predominate. The relatively high incidence of ring porous and semi-ring porous woods in India likely is correlated with the inclusion of Himalayan species and with c. 40% of India's forested land being tropical dry deciduous forests (Singh & Singh 1992; Kushwaha & Singh 2005).

Tangential vessel arrangement is a feature that is extremely rare in Tropical America, Tropical Africa, Southeast Asia, and Australia, and found at levels of 10% or more in Temperate Europe, Temperate Asia, North America and New Zealand (Table 2). Incidences of vessels in tangential bands and clusters are positively correlated with ring porosity. If a wood has tangential bands, the probabilities that it is ring porous (Table 3) and has vessels in clusters (Table 4) are much greater than by chance. The variation in distribution of these features by broad geographic area (Table 2) is consistent with previous documentation for the distribution of these features (*e.g.*, Baas *et al*. 1983; Carlquist & Hoekman 1985; Baas & Schweingruber 1987; Carlquist 1987, 2001).

The highest incidences (29%) of woods with vessels commonly in clusters are in the Mediterranean region and in New Zealand. The relatively high percentage for the

Table 3. Co-occurrence presence / absence of ring porosity and tangential bands.

| | Observed | Expected | % Deviation |
|---|---|---|---|
| Ring porous present<br>Tangential bands present | 89 | 11 | +677 |
| Ring porous present<br>Tangential bands absent | 195 | 273 | –28 |
| Ring porous absent<br>Tangential bands present | 136 | 213 | –36.1 |
| Ring porous absent<br>Tangential bands absent | 5195 | 5117 | +1.5 |

Table 4. Co-occurrence presence / absence of tangential bands and clusters.

| | Observed | Expected | % Deviation |
|---|---|---|---|
| Tangential bands present<br>Clusters present | 150 | 22 | +580 |
| Tangential bands present<br>Clusters absent | 75 | 203 | –63 |
| Tangential bands absent<br>Clusters present | 399 | 527 | –24 |
| Tangential bands absent<br>Clusters absent | 4991 | 4863 | +2.6 |

Mediterranean region is not surprising as Baas and Carlquist (1985) found very high incidences of vessel clusters in Mediterranean regions. New Zealand, except for the extreme north of North Island (which is almost subtropical), experiences frost and so might be considered cool temperate (Wardle 1991).

Diagonal / radial vessel arrangements are more common in the Northern Hemisphere than in Tropical America, India, and Asia; and are more common than expected by chance alone in ring porous woods than in diffuse porous woods (Table 5). However, the highest incidence of this feature is in Australia (26 %) where ring porosity is virtually non-existent. Approximately one-third of the records for Australia are species of Myrtaceae and Casuarinaceae, families that often have vessels in a radial or diagonal arrangement. Exclusively solitary vessels also characterize these two families and so the incidence of exclusively solitary vessels is also highest in Australia (37 %).

Table 5. Co-occurrence presence / absence of ring porosity and radial / diagonal vessel arrangement.

| | Observed | Expected | % Deviation |
|---|---|---|---|
| Ring porous present<br>Radial / diagonal arrangement present | 80 | 39 | +103 |
| Ring porous present<br>Radial / diagonal arrangement absent | 204 | 244 | –16.5 |
| Ring porous absent<br>Radial / diagonal arrangement present | 693 | 733 | –5.5 |
| Ring porous absent<br>Radial / diagonal arrangement absent | 4638 | 4597 | +0.9 |

***Perforation plates and Pits*** (Fig. 3, Table 2)

Simple perforation plates and alternate intervessel pits are the most common of all the hardwood features (Fig. 3). Almost certainly this high incidence reflects the hydraulic advantages of simple perforation plates over scalariform perforation plates in most environments (*e.g.*, Schulte 1999).

The incidences of exclusively simple, exclusively scalariform, and mixed simple and scalariform perforations vary by geographic region. Scalariform perforations have been suggested to have value in regions where freezing occurs, acting as a trap for air bubbles (Zimmermann 1983). Scalariform perforations are most common in Temperate Europe, Temperate Asia, North America, and New Zealand (all of which experience frost) and are especially rare in Madagascar (Table 2). Temperate South America has values as high or higher than most of the Tropics. The bulk of the records for this region is from Tortorelli's 1956 atlas of Argentinean woods, and includes subtropical to tropical elements. North American descriptions include some species from the arid southwest, the Mediterranean climate of California, and subtropical Florida, all regions that have a high incidence of simple perforations (Carlquist & Hoekman 1985).

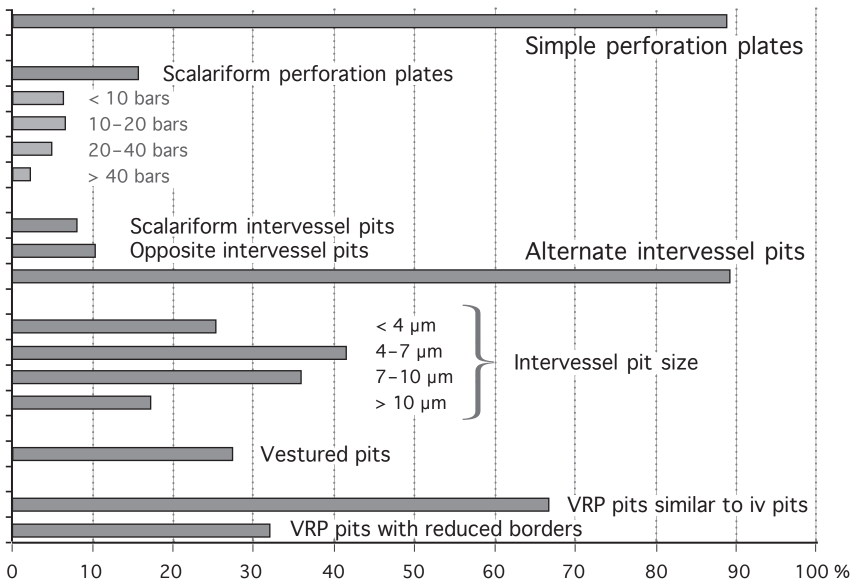



Figure 3. Incidences of perforation plate types and pitting features for the whole database.

Alternate intervessel pits likely have been selected for as the most structurally effective way to position breaks in the wall, with the equivalent of a honeycomb structure being stronger than pits arranged in horizontal rows (Carlquist 2001). Small to medium sized alternate intervessel pits are more common than either minute or large intervessel pits. Large alternate intervessel pits are the least common (Fig. 3). This raises the question whether there might be functional consequences of large intervessel pits and accompanying large pit membranes, which might be more likely than smaller pits to develop holes that would allow the spread of embolisms.

It has been hypothesized that vestured pits are important functionally as when a pit membrane deflects to the side of a pit chamber the vestures support the pit membrane and reduce the likelihood of its tearing and permitting the spread of embolisms (Zweypfennig 1978). The geographic distribution of vestured pits and their correlation with habitat has received considerable attention of late (*e.g.*, Jansen *et al.* 2003, 2004). Jansen *et al.* (2004) used data from the literature on the distribution and occurrence of vestured pits for 11,843 species and 6,428 genera, and found an overall frequency for vestured pits of 32%. For the whole of InsideWood database it is 28% (Fig. 3). Jansen *et al.* (2004) found considerable variation between macroclimate zones in the frequency of vestured pits. They are virtually absent from boreal and arctic areas, and at levels of 22% in cool temperate regions, 31% in everwet rainforests, and 50% in seasonal woodlands.

The InsideWood data also show geographic variation in the frequency of vestured pits (Table 2). Temperate Europe and Temperate Asia have low frequencies (<3% and 5%, respectively); North America as a whole has 12% vestured pits. These percentages are low compared to the 20–22% vestured pits for cool temperate regions that

Jansen *et al*. (2004) reported. This difference can be explained because one of the cool temperate floras they used was Australian. Australia is the geographic region with the highest percentage (37%) of vestured pits because of the high incidence of Myrtaceae; the temperate Australian flora they used was more speciose than the temperate Northern Hemisphere floras. Other percentages agree with what they reported. New Zealand, which was one of the cool temperate regions of Jansen *et al*., has 20% vestured pits. South Africa, Madagascar, Tropical Africa, India, and the Neotropics all have nearly 30%. Southeast Asia has a lower incidence than the other tropical regions, but this region has a relatively high incidence of woods with scalariform perforation plates, vestured pits and scalariform perforations hardly ever co-occur (Jansen *et al*. 2004). Temperate South America has a relatively high incidence of vestured pits (29%), in part due to a relatively high incidence of Leguminosae and likely because of the subtropical areas in that region. Although Jansen *et al*. (2004) did not find any variation in incidence of vestured pits by pit size, data from the InsideWood database indicate that vestured pits are less common in woods with large pits (18%) than in woods with medium (36%), small (36%), or minute pits (31%).

***Vessel-ray parenchyma pits***

Vessel-ray pits similar to intervessel pits are more common than vessel-ray pits with reduced borders (Fig. 3). There is geographic variation in the incidence of vessel-ray parenchyma pit types (Table 2). This is especially noticeable for vessel-ray parenchyma pits that have reduced borders and are horizontally or vertically elongated (Feature 32). This feature is not common in woods of the Mediterranean (15%) and North America (16%), and relatively common in woods of Southeast Asia (40%), Australia (44%), and New Zealand (44%). The percentage of this feature in woods of Temperate Asia (26%) is similar to the percentages found in Tropical Africa (28%), Madagascar (25%), and Temperate South America (27%), which is odd as usually the incidences of features of Temperate Asia are similar to Temperate Europe and North America, as would be expected because of shared taxa and broadly similar climates.

Chattaway (1949) and Bonsen and Kučera (1990) found that whether gums or tyloses were formed during heartwood formation or in response to injury was related to size of the aperture of vessel-ray parenchyma pits; woods with small vessel-ray parenchyma pits and small apertures form gums; woods with large vessel-ray parenchyma pits with large apertures form tyloses. An indirect way of looking at this relationship in the InsideWood database is to use the presence or absence of vessel-ray parenchyma pits similar to intervessel pits and vessel occlusion type (Table 6). The results are in accord with the observations of Chattaway and Bonsen and Kučera as there is a higher incidence of gums in woods with vessel-ray parenchyma pits similar to intervessel pits and a higher incidence of tyloses in woods in which vessel-ray parenchyma pits are not similar to intervessel pits.

***Helical thickenings*** (Table 2)

As expected, and shown by numerous workers for different datasets and within families and genera, there is geographic variation in the incidence of helical thickenings.

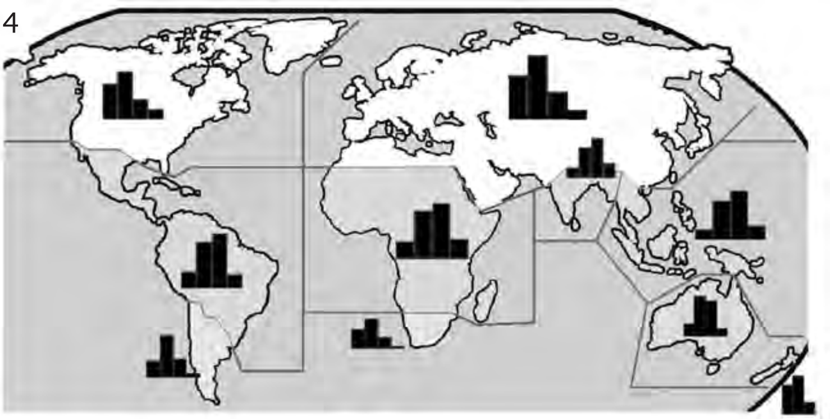
Table 6. Co-occurrence vessel-ray parenchyma pit type, tyloses, and gums.

| | Observed | Expected | % Deviation |
|---|---|---|---|
| Vessel-ray parenchyma pits similar<br>Tyloses present | 337 | 659 | –47.8 |
| Vessel-ray parenchyma pits similar<br>Gums present | 978 | 682 | +46.2 |
| Vessel-ray parenchyma pits NOT similar<br>Tyloses present | 733 | 411 | +72.9 |
| Vessel-ray parenchyma pits NOT similar<br>Gums present | 129 | 425 | –70.5 |

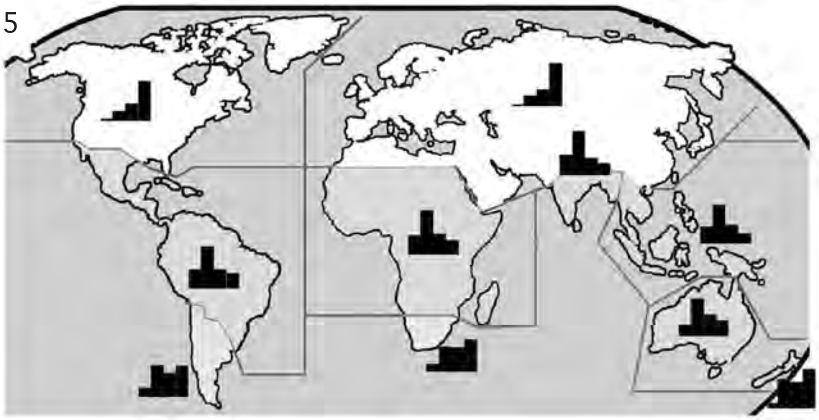
Feature 36 "vessels with helical thickenings" is relatively common in woods of the Northern Hemisphere (36–57%) and New Zealand (32%), and uncommon in tropical regions, being especially rare in Madagascar (< 2%, descriptions from Madagascar from P. Détienne, CIRAD), Tropical Africa (< 3%), and the Neotropics (< 4%). Temperate South America has an intermediate value of 13% (again, probably due to the mixture of temperate, subtropical and tropical woods described for Argentina by Tortorelli (1956)). Carlquist (2001) noted that helical thickenings are associated with regions that experience water stress created by drought or freezing. He suggested that in some way helical thickenings might diminish danger of cavitation, aid in refilling of vessels, or increase vessel wall strength.

***Quantitative vessel features*** (Fig. 4–6, Table 2)

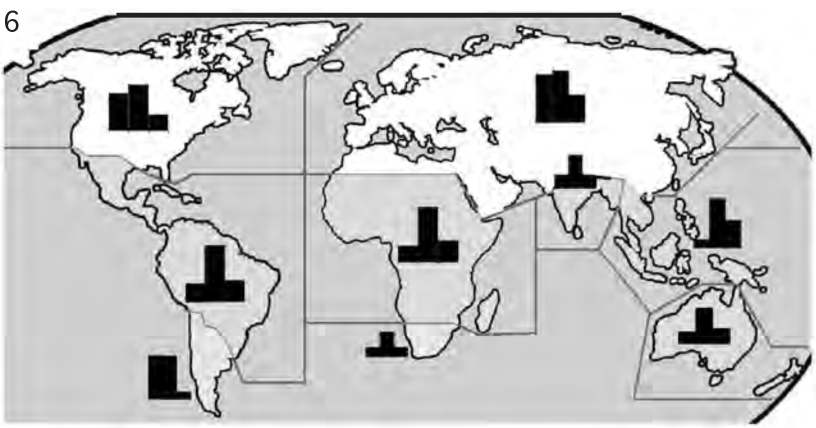
There is a considerable body of literature on the relationships of vessel diameter and density, one to another, and within different ecological regimes. These relationships have been examined within genera (*e.g.*, *Cornus,* Noshiro & Baas 2000; *Ilex*, Baas 1973; *Rhododendron,* Noshiro *et al.* 1995; *Symplocos*, Van den Oever *et al.* 1981), within families (*e.g.*, Cornaceae, Noshiro & Baas 1998; Rosaceae, Zhang *et al.* 1992), and across different geographic areas (*e.g.*, Carlquist 1977; Rury & Dickison 1984; Carlquist & Hoekman 1985; Wiemann *et al.* 1998, 1999). Within a tree, pith to bark, it has been observed that in diffuse porous woods, vessel diameter increases and vessel density concomitantly decreases during the juvenile wood period (Panshin & De Zeeuw 1980). On the basis of these numerous studies it is expected that there often is a near inverse, but non-linear, relationship between diameter and density. Few, wide vessels are associated with humid environments at lower latitudes and are rare at high latitudes, while many narrow vessels are associated with high latitudes, and environments (desert, arctic, alpine) with prolonged periods of low water availability. Here we present data for those features on a broad geographic basis. This inverse relationship between diameter and density is one aspect of examining tradeoffs between transport efficiency and safety from cavitation (Zimmermann 1983; Tyree *et al.* 1994; Baas *et al.* 2004).




Vessel diameter classes: < 50 µm, 50–100 µm, 100–200 µm, ≥ 200 µm




Vessels per square mm: < 5, 5–20, 20–40, 40–100, > 100




Vessel element length: < 350 µm, 350–800 µm, > 800 µm

Figures 4–6. Geographic distribution patterns of quantitative vessel element features. – 4: Mean vessel diameter classes (includes diffuse porous, semi-ring porous, and ring porous woods). – 5: Vessels per sq. mm (only diffuse porous woods). – 6: Vessel element lengths.

*Vessel diameter* — Figure 4 shows the geographic distribution of mean vessel diameter classes. Temperate North America, Temperate Asia and Temperate Europe have similar patterns, with relatively high incidences of narrow and very narrow vessels. In these regions, the woods with tangential diameters of more than 200 µm are ring porous. Mean tangential diameters of 200 µm are virtually absent from Temperate South America, South Africa, and New Zealand, regions with very few ring porous woods. Distributions of vessel diameter classes are similar for Tropical America, Tropical Africa, Southeast Asia, and India (Fig. 4).

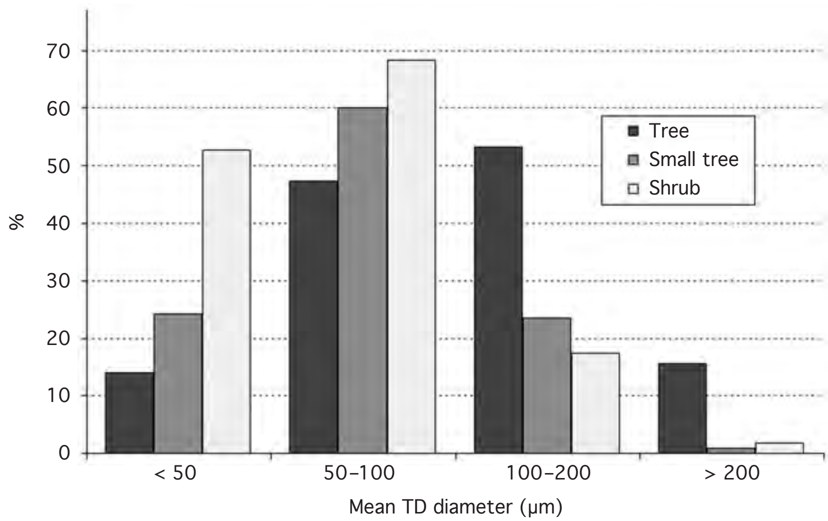



Figure 7. Incidences of mean tangential diameter classes for trees, small trees, and shrubs.

Mean vessel diameter is related to habit as well as to geographic region. Figure 7 shows the relative proportion of each vessel diameter class for trees, small trees, and shrubs. Shrubs have the highest proportion of very narrow vessels (< 50 µm) whereas wide vessels (> 200 µm in diameter) are virtually absent. Therefore, we can infer that an isolated piece of fossil wood with vessel diameters close to 200 µm likely would be a tree, as was done for a phyllanthoid fossil wood from the Edwards Limestone of Aptian-Albian age (Wheeler 1991).

*Vessel density* — Strictly from a packing standpoint, if one assumed that there was a fixed proportion of cross-sectional area that would be occupied by vessels, then woods with wide vessels should have fewer vessels per square mm than woods with narrow vessels. Woody climbers constitute an exception to the rule, as they often combine very wide vessels with fairly high vessel densities. Given that conductivity is proportional to the 4$^{th}$ power of the radius of the conduit, then few wide vessels can conduct more water than many narrow vessels (Zimmermann 1983). It has thus been proposed that there is a tradeoff between efficiency (wide vessels) and safety (narrow vessels) (Zimmermann 1983; Baas *et al.* 2004). On a large geographic scale, averaged across many clades, data from the InsideWood site support such a tradeoff. Woody plants of North

America, Temperate Asia and Europe have traded efficiency for safety as woods with narrow vessels (Fig. 4) and more than 40 vessels per sq. mm (Fig. 5) are common. In contrast, woody plants of Tropical America, Tropical Africa, Southeast Asia, and India mostly have 5–20 vessels per sq. mm and vessels > 100 μm; in other words, woods that are less safe, but more efficient (Fig. 4 & 5).

*Vessel element lengths* — Again, there is a difference in the patterns of tropical and temperate regions (Fig. 6). North America and Temperate Asia and Europe have similar vessel element length distribution patterns; Tropical America, Tropical Africa, and Central Asia share similar vessel element length distribution patterns. Although incidences of vessel diameter and density in Southeast Asia are similar to the other equatorial regions, there is a higher incidence of long vessel elements in Southeast Asia, which likely is related to there being a higher incidence of woods with exclusively scalariform perforation plates in Southeast Asia (13 %) than in Tropical America (7 %) or Tropical Africa (6 %) (Table 2).

Just as vessel diameter and vessel density are related to habit, so is vessel element length, as found for Cornaceae (Noshiro & Baas 1998, 2000). The incidences of vessel element length categories within geographic regions are related to the incidences of shrubs in each region (Table 2). The geographic region (Mediterranean Europe) that has the highest incidence of short vessel elements (77 %) is the region that has the highest percentage of shrubs (72 %).

The functional advantages of vessel element length variations are not as established as are the functional advantages of variations in vessel diameter. Vessel element lengths reflect fusiform initial lengths. What would be the advantages of short fusiform initials? One speculation is that cambial division and the production of new cells would be more rapid for short fusiform initials than for long ones, and so would be advantageous in regions with short growing reasons. The general distribution pattern of vessel element lengths is consistent with that hypothesis, but we know relatively little about relative rates of cell production.

***Imperforate elements / Fibers*** (Fig. 8)

*Vascular and vasicentric tracheids* — Vascular and vasicentric tracheids are grouped together as one feature in the IAWA Hardwood List, so it is not possible to directly use the database to evaluate the degree to which each is correlated with other features. Jointly, they are much less common in tropical regions than in temperate and Mediterranean regions (Table 2). It has been suggested that vasicentric tracheids would be associated with woods with medium to large exclusively solitary vessels; vascular tracheids, which have been defined as “degenerate vessel elements” are expected to be associated with vessels in clusters (Carlquist 1984, 1985, 2001). The observed co-occurrence of vascular/vasicentric tracheids and these vessel features is higher than would be expected than by chance (Tables 7 & 8) and thus supports Carlquist’s expectations. No doubt the co-occurrences would be higher if the two tracheid types had been recorded separately.

*Fiber pits* — Simple to minutely bordered fiber pits are more common than distinctly bordered fiber pits. Simple to minutely bordered fiber pits are present in more than 70 %

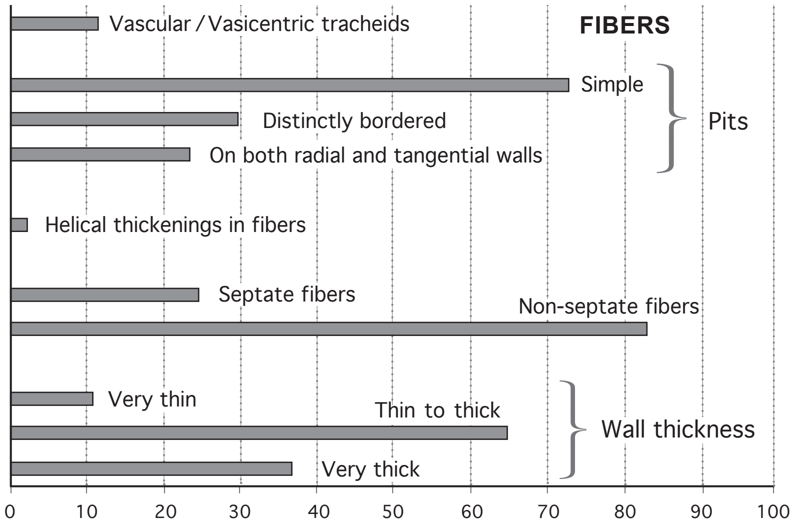



Figure 8. Incidence of imperforate element features for the whole database.

Table 7. Co-occurrence presence / absence exclusively solitary vessels more than >100 μm diameter and vascular / vasicentric tracheids.

| | Observed | Expected | % Deviation |
|---|---|---|---|
| Exclusively solitary vessels, TD >100<br>Tracheids present | 149 | 35 | +325 |
| Exclusively solitary vessels, TD >100<br>Tracheids NOT present | 135 | 249 | –46 |
| NOT Exclusively solitary vessels, TD >100<br>Tracheids present | 143 | 257 | –7 |
| NOT Exclusively solitary vessels, TD >100<br>Tracheids NOT present | 1951 | 1836 | +2 |

Table 8. Co-occurrence presence / absence of vessel clusters and vascular / vasicentric tracheids.

| | Observed | Expected | % Deviation |
|---|---|---|---|
| Clusters present<br>Tracheids present | 146 | 70 | –106.4 |
| Clusters present<br>Tracheids absent | 403 | 478 | –15.7 |
| Clusters absent<br>Tracheids present | 575 | 650 | –11.5 |
| Clusters absent<br>Tracheids absent | 4491 | 4415 | +1.7 |

of the woods of the Mediterranean (76%), India (78%), Southeast Asia (71%), Tropical Africa and Madagascar (both 79%), South Africa (71%), the Neotropics (79%), and Temperate South America (82%). Temperate Europe and Temperate Asia have the lowest percentages of simple to minutely bordered fiber pits, at 54% and 55%, respectively. Somewhat surprisingly, the percentage of North American woods, 67%, is higher. Australia has the lowest percentage (52%), but Myrtaceae often have distinctly bordered fiber pits, and they are a large component of the Australia flora. New Zealand, with 63% simple to minutely bordered fiber pits, is intermediate.

*Septate fibers* — Septate fibers are living fibers whose functions are assumed to be similar to those of axial parenchyma. Thus, it has been suggested that woods with septate fibers are unlikely to have abundant axial parenchyma (*e.g.*, Carlquist 2001). Carlquist noted that Harrar's 1946 work supported that expectation, but Frison (1948) disagreed with that generalization. The data drawn from the InsideWood database (Table 9) indicate that woods in which axial parenchyma is rare to absent have a significantly higher incidence of septate fibers than expected, supporting the generalizations of Harrar (1946) and Carlquist (2001). Axial parenchyma occurs in some woods with septate fibers, but it is difficult to evaluate its abundance using just categories of parenchyma distribution. However, analysis of the list of woods that have septate fibers but do not have the feature "axial parenchyma rare", shows over 80% of those woods have scanty paratracheal to vasicentric parenchyma, rather than more elaborate forms of parenchyma. Septate fibers are less common in the temperate Northern Hemisphere than in the tropics and most regions of the Southern Hemisphere, with the incidence in Australia being intermediate (Table 2).

Table 9. Co-occurrence presence / absence of rare axial parenchyma and septate fibers.

| | Observed | Expected | % Deviation |
|---|---|---|---|
| Axial parenchyma rare<br>Septate fibers present | 504 | 205 | +146 |
| Axial parenchyma rare<br>Septate fibers absent | 287 | 586 | –51 |
| "Axial parenchyma rare" absent<br>Septate fibers present | 942 | 1241 | –24 |
| "Axial parenchyma rare" absent<br>Septate fibers absent | 3857 | 3558 | +8 |

*Fiber wall thickness* — Very thick-walled fibers are more common than very thin-walled fibers. The highest incidences of very thin-walled fibers is in Temperate Europe and Southeast Asia (18%), the lowest is in South Africa (5%). Nearly half of the woods of Tropical Africa (48%) and South Africa (46%) have very-thick-walled fibers (Table 2).

Ewers (in Baas *et al.* 2004) prepared a diagram of a tradeoff triangle of wood functions and associated anatomical features, the points of the triangle being 1) resistance to embolism (narrow vessels), 2) conductive efficiency (wide vessels), and 3) mechanical strength (thick-walled fibers). It was proposed that there was a negative relationship between mechanical strength and conductive efficiency and a positive relationship between mechanical strength and safety. Some studies have found a positive correlation between wood density and resistance to cavitation (Hacke *et al.* 2001; Jacobsen *et al.* 2005). Presumably woods with thick-walled fibers have thick-walled vessels. High density woods are common in arid regions (Chudnoff 1976), where there would be greater negative xylem pressures and a greater need for vessel wall reinforcement (Hacke *et al.* 2001). The functional consequences of variation in pit morphology, including membrane characteristics, and their relationship to thick-walled vessels is an area of continued interest (Hacke *et al.* 2006; Sperry *et al.* 2006).

Figure 9 presents data on the incidence of fiber wall thickness classes by vessel diameter classes. It shows a weak but consistent trend for the incidence of thin-walled fibers to increase with increasing vessel diameter while the incidence of very-thick-walled fibers decreases with increasing vessel diameter. These trends are consistent with what would be proposed by the tradeoff triangle. Note, however, that a majority of taxa have "thin- to thick-walled fibres" and all vessel diameter categories are equally well represented.

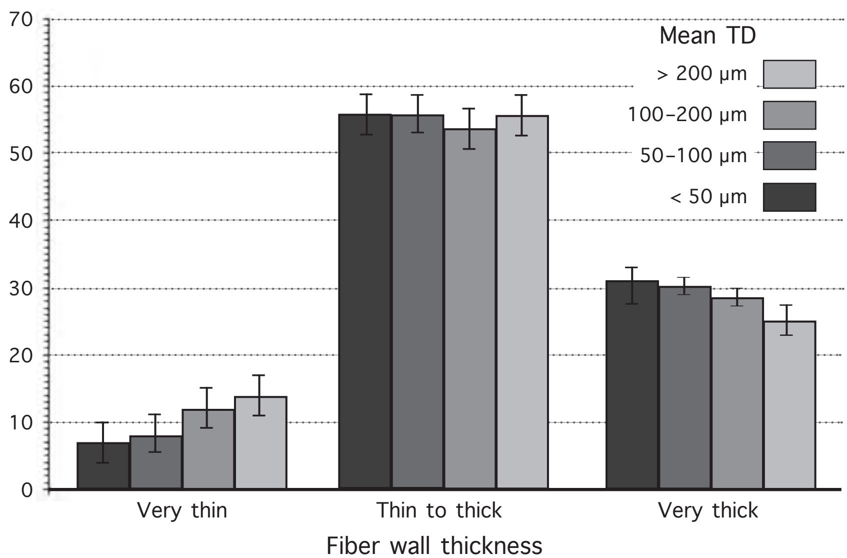



Figure 9. Incidence of fiber wall classes within different mean tangential diameter classes.

***Axial parenchyma*** (Fig. 10)

Axial parenchyma features are more balanced in occurrence than are qualitative vessel features. The only feature that occurs in more than 50 % of the InsideWood descriptions is axial parenchyma strands of 3–4 cells (Table 2).

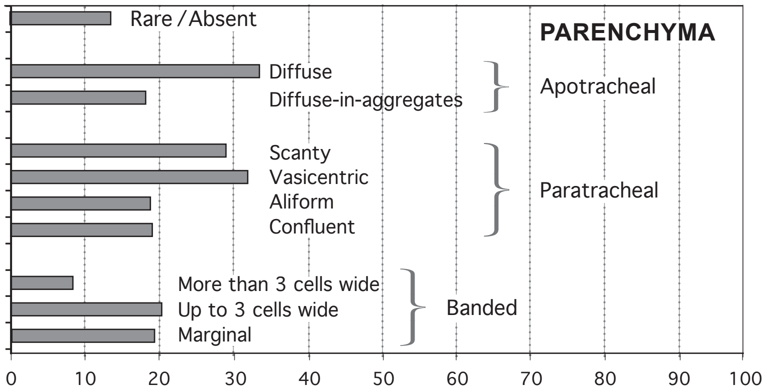



Figure 10. Incidence of axial parenchyma features within the whole database.

Elaborate axial parenchyma patterns, *e.g.*, aliform to confluent parenchyma and wide bands of axial parenchyma, are more common in the tropics than in the temperate regions. Aliform parenchyma occurs in less than 5 % of the records for New Zealand and Temperate Europe, and in 20 % or more of the records for India, Southeast Asia, Tropical Africa, Madagascar, and the Neotropics. Axial parenchyma bands more than 3 cells wide are especially rare in Temperate Europe, Temperate Asia, and North America (< 3 %) and are in 9–15 % of the records of the Tropics, with a maximum incidence in Madagascar.

Relative to our understanding of the functional significance of variations in vessel size, little has been established as to the advantages that different axial parenchyma patterns might confer. Parenchyma typically is referred to as serving a storage function, for both water and carbohydrates. It is also important in biologic defense mechanisms. Living parenchyma manufactures secondary metabolites, but to our knowledge, whether there is a relationship between extractive content and axial parenchyma abundance or type has not been analyzed. In the past, it was suggested that abundant paratracheal parenchyma could help to refill air-filled vessels or might act as an osmotic pump to "push" water up the vessel in regions where atmospheric humidity is high (*e.g.*, Braun 1984) or aid in the recovery from embolism (Salleo *et al.* 2004). When parenchyma content is especially high, it affects the biomechanical properties of the wood (*e.g.*, Chapotin *et al.* 2006). For woods of similar specific gravity classes, ones with broad parenchyma bands have a somewhat lower stiffness than woods without them (data from Chudnoff 1984, analyzed by J. Wilder, unpublished student project paper, N.C. State University).

***Ray characteristics*** (Fig. 11)

None of the IAWA ray features occur in more than 50 % of the descriptions; four occur in fewer than 10 % of the descriptions. There do not appear to be any clear geographical or ecological trends in the ray features considered, so it is tempting to examine whether they have systematic value. Three of these four uncommon ray features have

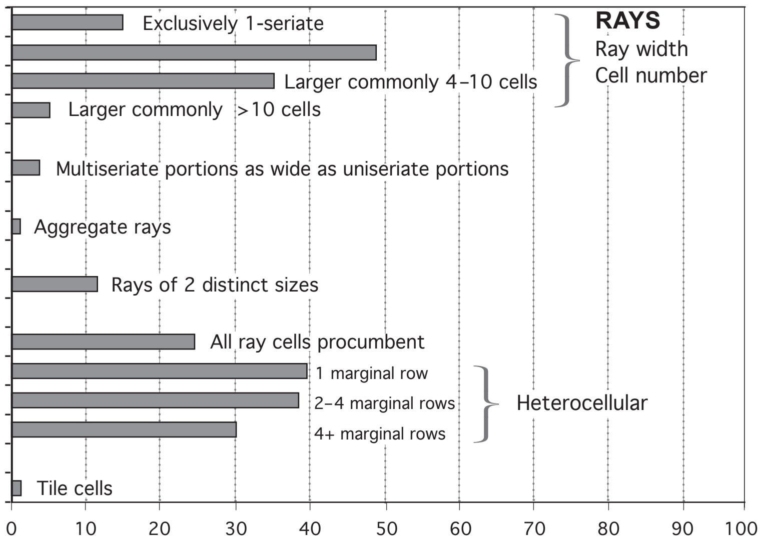



Figure 11. Incidence of ray features within the whole database.

restricted occurrence: 1) tile cells occur in the Malvales, 2) rays with the multiseriate portions as wide as the uniseriate portions are most commonly found in families within the Gentianales (Apocynaceae and Rubiaceae), Malpighiales, and Myrtales, and 3) aggregate rays occur primarily in the Fagales, with scattered reports of a few species with aggregate rays or tendencies to form aggregate rays in other families. There are, to our knowledge, no reasonable hypotheses for the functional significance of tile cells, aggregate rays, or rays in which the narrow multiseriate portions are of the same width as the uniseriate portion.

The fourth uncommon ray feature, rays wider than 10-seriate, is considerably more widespread, occurring in 83 families spanning 31 orders, with 3 families not placed in an order. This count uses the family/order placement from Stevens (2001 onwards). Carlquist (2001) provided a list of families with "Very wide rays (about six cells wide or more, including aggregate rays and rays representing extensions of primary rays." The list of families with rays more than 10-seriate taken from InsideWood differs somewhat from Carlquist's list, which was modified from Yatsenko-Khmelevsky (1954); in part because the criterion for 'very wide rays' differs, in part, because of changes in family structure because of recent phylogenetic analysis (APG II), but a few families with species with "very wide rays" seem to have been overlooked, *e.g.*, Capparaceae, Celastraceae, Elaeagnaceae, Menispermaceae, Salvadoraceae. Orders in which most, if not all, woody families have species with very wide rays are Aquifoliales, Proteales, Ranunculales, and Vitales. Wide rays are an anatomical feature that supports the placement of the Platanaceae and Proteaceae in the same order, Proteales. Vines often have wide rays (Carlquist 1991), so most families with woody vines have species with rays wider than 10-seriate. It has been suggested that wide rays are advantageous for vines, especially when the ray cells are thin-walled and unlignified, as this provides flexibility, and increases ability to respond to wounds and to regenerate after tree fall (Fisher & Ewers 1989; Carlquist 1991). We also found the incidence of wide rays to be somewhat more common in shrubs than expected (Table 10).

Table 10. Co-occurrence presence / absence of rays commonly >10-seriate with shrubs / trees.

| | Observed | Expected | % Deviation |
|---|---|---|---|
| Shrub<br>Rays >10-seriate | 106 | 75 | +41 |
| Shrub<br>Rays less than 10-seriate | 1222 | 1253 | –2.5 |
| Tree<br>Rays >10-seriate | 244 | 275 | –11 |
| Tree<br>Rays less than 10-seriate | 4653 | 4622 | +0.7 |

***Storied structure***

Storied rays are not common, with the highest incidences in Madagascar (11%) and temperate South America (7%) (regions with the lowest incidence of tall rays > 1 mm high, 11% and 17%, respectively). Temperate South America has a high proportion of papilionoid legumes, a clade with a high incidence of storied structure. Storied axial parenchyma is more than twice as common as storied rays, and most common in the Mediterranean, the region with highest incidence of fusiform axial parenchyma cells. Woods of the Mediterranean and Temperate Europe rarely have storied rays (0.5%), but have relatively high incidences of storied axial parenchyma (22% and 15%, respectively).

***Inclusions*** (Table 2)

The lowest incidences of prismatic crystals are in Temperate Europe (20%) and New Zealand (24%), with the highest incidences in South Africa (58%), Tropical Africa (59%), and Madagascar (61%). There is a general trend of increasing incidence of crystals from temperate to tropical regions, and for relatively high occurrences in regions that are largely xeric (the Mediterranean and Australia). When crystals are present, they are most commonly located in upright/square ray cells and chambered axial parenchyma cells. Crystals in enlarged cells are more common in the Northern Hemisphere (Europe, Asia, North America) than in other regions. The occurrence of silica bodies is predominantly a tropical feature, but somewhat anomalously temperate South America has the highest incidence (11%). This region is a mixture of environments and its family and generic composition is similar to the Neotropics, which has an incidence of 10%.

## DISCUSSION AND CONCLUSIONS

1) This overview of the content of the InsideWood database provides information on the relative abundances of selected wood anatomical features, within woody dicots as a whole, and within broad geographic regions. In terms of vessel features, it is apparent that the most common suite of features is diffuse porosity, randomly arranged vessels that are solitary and in short multiples, simple perforations, and alternate intervessel pits. Some uncommon features are restricted to but one or a few orders (*e.g.*, tile cells, rays with multiseriate portion(s) as wide as uniseriate portions), but others (*e.g.*, large rays commonly more than 10-seriate) occur across many orders.

2) The non-random patterns of geographic distribution of many vessel element features are consistent with the ecological trends established in numerous studies. The non-random distribution patterns of other features, such as vessel-ray parenchyma pitting type and fusiform parenchyma, invite further investigation as to their ecophyletic and ecophysiological significance. It is also apparent that robust statistical tests need to be applied to determine the levels of significance of differences in distribution patterns and feature correlations, and to identify suites of correlated features, other than the classic "primitive" or "derived" features of Frost and Bailey. Also, determining which features do not co-occur could inform investigations of wood anatomical variation and development.

3) This overview is not an integral analysis that takes into account phylogenetic constraints and explores how observed variations in geographic distribution of features are related to which clades are abundant in a given region. That such considerations may be important is apparent from the incidence of many features in Australia being the result of the Myrtaceae being an important component of the Australian flora.

4) The InsideWood database is a resource for further studies. Including detailed information on the ecologic and geographic range of each species and on vessel diameter, density, and cell lengths would help advance the use of wood anatomical features as proxies for macroclimate and ecology. This would have value for interpreting fossil wood assemblages and tracing the ecophysiological history of woody dicots. The database also can be used to investigate how wood anatomical patterns vary within families and orders.

## ACKNOWLEDGEMENTS

NSF Grants BRC 0237368 and DBI / BDI 0518386 to N.C. State University supported the development of the InsideWood web site. We thank Pierre Détienne, CIRAD, for providing descriptions of Madagascar woods; Carolyn Argentati, Kristin Entelman, and Susan Nutter of the NCSU Libraries administration for their continued support, Jeff Bartlett for contributions to the development of the database and Troy Simpson for programming; Mike Wiemann, Uwe Hacke, and Steven Jansen for their reviews of the manuscript.

## REFERENCES

APG [= Angiosperm Phylogeny Group] II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.

Baas, P. 1973. The wood anatomical range in *Ilex* (Aquifoliaceae) and its ecological and phylogenetic significance. Blumea 21: 193–258.
Baas, P. 1986. Ecological patterns of xylem anatomy. In: J. Givnish (ed.), On the economy of plant form and function: 327–352. Cambridge University Press, Cambridge, New York.
Baas, P. & S. Carlquist. 1985. A comparison of the ecological wood anatomy of the floras of southern California and Israel. IAWA Bull. n.s. 6: 349–353.
Baas, P., F.W. Ewers, S.D. Davis & E.A. Wheeler. 2004. The evolution of xylem physiology. In: A.R. Hemsley & I. Poole (eds.), Evolution of plant physiology. From whole plants to ecosystems: 273–296. Linnaean Society Symposium Series No. 21. Elsevier Academic Press.
Baas, P. & F.H. Schweingruber. 1987. Ecological trends in the wood anatomy of trees, shrubs and climbers from Europe. IAWA Bull. n.s. 8: 245–274.
Baas, P., E. Werker & A. Fahn. 1983. Some ecological trends in vessel characters. IAWA Bull. n.s. 4: 141–159.
Bissing, D.R. 1982. Variation in qualitative anatomical features of the xylem of selected dicotyledonous woods in relation to water availability. Bull. Torrey Bot. Club 109: 371–384.
Bonsen, K.J.M. & L.J. Kučera. 1990. Vessel occlusions in plants: morphological, functional and evolutionary aspects. IAWA Bull. n.s. 11: 393–399.
Braun, H.J. 1984. The significance of accessory tissues of the hydrosystem for osmotic water shifting as the second principle of water ascent, with some thoughts concerning the evolution of trees. IAWA Bull. n.s. 5: 275–294.
Brazier, J.D. & G.L. Franklin. 1961. Identification of hardwoods. A microscope key. Forest Products Research Bulletin No. 46. 96 pp.
Carlquist, S. 1975. Ecological strategies of xylem evolution. University of California Press, Berkeley. 259 pp.
Carlquist, S. 1977. Ecological factors in wood evolution: a floristic approach. Amer. J. Bot. 64: 887–896.
Carlquist, S. 1984. Vessel grouping in dicotyledon wood: significance and relationship to imperforate tracheary elements. Aliso 10: 505–525.
Carlquist, S. 1985. Vasicentric tracheids as a drought survival mechanism in the woody flora of southern California and similar regions: review of vasicentric tracheids. Aliso 11: 37–68.
Carlquist, S. 1987. Diagonal and tangential vessel aggregations in wood: function and relationship to vasicentric tracheids. Aliso 11: 451–462.
Carlquist, S. 1991. Anatomy of vine and liana stems: a review and synthesis. In: R.E. Putz & H. Mooney (eds.), The biology of vines: 53–71. Cambridge University Press.
Carlquist, S. 2001. Comparative wood anatomy. Systematic, ecological, and evolutionary aspects of dicotyledon wood. 2nd Ed. Springer. 448 pp.
Carlquist, S. & D.A. Hoekman. 1985. Ecological wood anatomy of the woody southern California flora. IAWA Bull. n.s. 6: 319–347.
Chapotin, S.M., J.H. Razanameharizaka & N.M. Holbrook. 2006. A biomechanical perspective on the role of large stem volume and high water content in baobab (*Adansonia* spp.; Bombacaceae). Amer. J. Bot. 93: 1251–1264.
Chattaway, M.M. 1949. The development of tyloses and secretion of gum in heartwood formation. Aust. J. Sci. Res. B 2: 227–240.
Chudnoff, M. 1976. Density of tropical timbers as influenced by climatic life zones. Commonwealth For. Rev. 55: 203–217.
Chudnoff, M. 1984. Tropical timbers of the World. USDA Agriculture Handbook 607. Madison, WI.
Clarke, S.H. 1936. A multiple-entry perforated-card key with special reference to the identification of hardwoods. New Phytologist 37: 369–374.
Détienne, P. & P. Jacquet. 1983. Atlas d'identification des bois de l'amazonie et des regions voisines. Centre Technique Forestier Tropical, Nogent s/Marne. 640 pp.
Ewers, F.W. 1985. Xylem structure and water conduction in conifer trees, dicot trees, and lianas. IAWA Bull. n.s. 6: 309–317.

Fahn, A., E. Werker & P. Baas. 1986. Wood anatomy and identification of trees and shrubs from Israel and adjacent regions. Israel Academy of Sciences and Humanities. 221 pp.
Fisher, J.B. & F.W. Ewers. 1989. Wound healing in stems of lianas after twisting and girdling. Bot. Gaz. 150: 251–265.
Frison, E. 1948. De la presénce d'amidon dans le lumen des fibres du bois. Bull. Agric. Congo Belge 39: 869–874.
Frost, F.H. 1930. Specialization of secondary xylem in dicotyledons. II. Evolution of end wall of vessel segments. Bot. Gaz. 90: 198–212.
Frost, F.H. 1931. Specialization of secondary xylem in dicotyledons. III. Specialization of lateral wall of vessel segments. Bot. Gaz. 91: 88–96.
Gilbert, S.G. 1940. Evolutionary significance of ring porosity in woody angiosperms. Bot. Gaz. 102: 105–120.
Gregory, M. 1994. Bibliography of systematic wood anatomy of dicotyledons. IAWA J., Suppl. 1. 265 pp.
Hacke, U.G., J.S. Sperry, W.T. Pockman, S.D. Davis & K.A. McCulloch. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126: 457–461.
Hacke, U.G., J.S. Sperry, J.K. Wheeler & L. Castro. 2006. Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiology 26: 689–701.
Harrar, E.S. 1946. Notes on starch grains in septate fiber-tracheids. Trop. Woods 85: 1–9.
IAWA Committee. 1989. IAWA List of microscopic features for hardwood identification. IAWA Bull. n.s. 10: 219–332.
Jacobsen, A.L., F.W. Ewers, R.B. Pratt, W.A. Paddock III & S.D. Davis. 2005. Do xylem fibers affect vessel cavitation resistance? Plant Physiology 139: 546–556.
Jansen, S., P. Baas, P. Gasson, F. Lens & E. Smets. 2004. Variation in xylem structure from tropics to tundra: Evidence from vestured pits. Proc. Nat. Acad. Sci. 101 (23): 8833–8837.
Jansen, S., P. Baas, P. Gasson & E. Smets. 2003. Vestured pits: do they promote safer water transport? Int. J. Plant Sci. 164: 405–413.
Kushwaha, C.P. & K.P. Singh. 2005. Diversity of leaf phenology in a tropical deciduous forest in India. J. Tropical Biology 21: 47–56.
LaPasha, C.A. & E.A. Wheeler. 1987. A microcomputer based system for computer-aided wood identification. IAWA Bull. n.s. 8: 347–354.
Lens, F. 2005. Systematic significance of wood anatomical characters in Ericales. PhD Thesis. Laboratorium voor Systematiek, K.U. Leuven, Belgium. 290 pp.
Lens, F., J.L. Luteyn, E. Smets & S. Jansen. 2004. Ecological trends in the wood anatomy of Vaccinioideae. Flora 199: 309–319.
Metcalfe, C.R. & L. Chalk. 1950. Anatomy of the Dicotyledons. Vols I & II. Oxford, Clarendon Press. 1500 pp.
Normand, D. & J. Paquis. 1976. Manuel d'identification des bois commonciaux. Tome 2. Afrique guineo-congolaise. Centre Technique Forestier Tropical, Nogent s/Marne. 335 pp.
Noshiro, S. & P. Baas. 1998. Systematic wood anatomy of Cornaceae and allies. IAWA J. 19: 43–97.
Noshiro, S. & P. Baas. 2000. Latitudinal trends in wood anatomy within species and genera: Case study in *Cornus* s.l. Amer. J. Bot. 87: 1495–1506.
Noshiro, S., M. Suzuki & H. Ohba. 1995. Ecological wood anatomy of Nepalese *Rhododendron*. I. Interspecific variation. J. Plant Research 108: 1–9.
Panshin, A.J. & C. DeZeeuw. 1980. Textbook of wood technology: structure, identification, properties, and uses of the commercial woods of the United States and Canada. 4th Ed. McGraw-Hill, New York. 722 pp.
Pearson, R.G. & E.A. Wheeler. 1981. Computer identification of hardwood species. IAWA Bull. n.s. 2: 37–40.
Poole, I., H.G. Richter & J.E. Francis. 2000. Evidence for Gondwanan origins for *Sassafras* (Lauraceae)? Late Cretaceous fossil wood of Antarctica. IAWA J. 21: 463–475.

Rodgers, S., E. Wheeler, T. Simpson & J. Bartlett. 2005. Integrating image-rich biological information with a web-search tool. The InsideWood model. TCDL Bulletin 2 (1) http://www.ieee-tcdl.org/Bulletin/v2n1/rodgers/rodgers.html
Rury, P.M. & W.C. Dickison. 1984. Structural correlations among wood, leaves and plant habit. In: R.A. White & W.C. Dickison (eds.), Contemporary problems in plant anatomy: 495–540. Academic Press, Orlando, Florida.
Salleo, S., M.A. Lo Gullo, P. Trifilô & A. Nardini. 2004. New evidence for a role of vessel-associated cells and phloem in the rapid xylem refilling of cavitated stems of *Laurus nobilis* L. Plant, Cell & Environment 27: 1065–1076.
Schulte, P.J. 1999. Water flow through a 20-pore perforation plate in vessels of *Liquidambar styraciflua*. J. Exp. Bot. 50: 1179–1187.
Singh, J.S. & V.K. Singh. 1992. Phenology of seasonally dry tropical forest. Current Science 63: 684–688.
Sperry, J.S. & U.G. Hacke. 2004. Analysis of circular bordered pit function. I. Angiosperm vessels with homogeneous pit membranes. Amer. J. Bot. 91: 369–385.
Sperry, J.S., U.G. Hacke & J. Pitterman. 2006. Size and function in conifer tracheids and angiosperm vessels. Amer. J. Bot. 93: 1490–1500.
Stevens, P.F. 2001 onwards. Angiosperm Phylogeny Website. Version 7, May 2006 [and more or less continuously updated since]. http://www.mobot.org/MOBOT/research/APweb/.
Ter Welle, B.J.H., J. Koek-Noorman & S.M.C. Topper. 1986. The systematic wood anatomy of the Moraceae (Urticales). IV. Genera of the Tribe Moreae with urticaceous stamens. IAWA Bull. n.s. 7: 91–128.
Terrazas, T. S. 1994. Wood anatomy of the Anacardiaceae: ecological and phylogenetic interpretation. Unpublished PhD dissertation, University of North Carolina at Chapel Hill. 321 pp.
Tortorelli, L.A. 1956. Maderas y bosques argentinos. Editorial Acme, Buenos Aires. 910 pp.
Tyree, M.T., S.D. Davis & H. Cochard. 1994. Biophysical perspectives of xylem evolution – is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? IAWA J. 15: 335–360.
Van den Oever, L., P. Baas & M. Zandee. 1981. Comparative wood anatomy of *Symplocos* and latitude of provenance. IAWA Bull. n.s. 23: 3–24.
Wardle, P. 1991. Vegetation of New Zealand. Cambridge University Press, Cambridge. 672 pp.
Wheeler, E.A. 1991. Paleocene dicotyledonous trees from Big Bend National Park, Texas. Variability in wood types common in the Late Cretaceous and Early Tertiary, and ecological inferences. Amer. J. Bot. 78: 658–671.
Wheeler, E.A., R.G. Pearson, C.A. LaPasha, W. Hatley & T. Zack. 1986. Computer-aided wood identification. Station Bulletin No. 474, N.C. Ag. Res. Serv., Raleigh, N.C. 160 pp.
Wiemann, M.C., S.R. Manchester & E.A. Wheeler. 1999. Paleotemperature estimation from dicotyledonous wood anatomical characters. Palaios 14: 459–474.
Wiemann, M.C., E.A. Wheeler, S.R. Manchester & K.M. Portier. 1998. Dicotyledonous wood anatomical characters as predictors of climate. Palaeogeography, Palaeoclimatology, Palaeoecology 139: 83–100.
Worbes, M. 1989. Growth rings, increment and age of trees in inundation forests, savannas, and a mountain forest in the Neotropics. IAWA Bull. n.s. 10: 109–122.
Worbes, M. 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. J. Ecology 87: 391–403.
Yatsenko-Khmelevsky, A.A. 1954. Research and methods of anatomical investigation of woody plants. Isdatelistvo Akademii Nauk SSR, Moscow. 337 pp. [In Russian]
Zhang, S-Y., P. Baas & M. Zandee. 1992. Wood structure of the Rosaceae in relation to ecology, habit and phenology. IAWA Bull. n.s. 13: 307–349.
Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer, New York. 143 pp.
Zweypfennig, R.C.V.J. 1978. A hypothesis on the function of vestured pits. IAWA Bull. 1: 13–15.